ON THE HABITS OF THE CRUSTACEANS FOUND IN CHÆTOPTERUS TUBES AT WOODS HOLE, MASSACHUSETTS.

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Among the numerous species of crustaceans which live as commensals, three interesting representatives occur in the leathery tubes of the worm *Chætopterus variopedatus* Renier et Claparède, at Woods Hole. The tubes of this annelid are U-shaped and taper toward the round opening at either end (Fig. 7). The tips of the tube may be seen protruding above the mud in open shallow water where eel-grass grows. Enders ('05, '09) has published two papers describing the habits of *Chætopterus* and its commensals as he observed them at Beaufort, North Carolina. Van Beneden ('76, p. 20) also mentions a worm, which is doubtless the same, as associated with crabs on the coast of Brazil. While occupying a room in the Marine Biological Laboratory during the past summer I was able to verify Ender's work and to add some new observations. My thanks are due to the staff of the laboratory for their courtesy, particularly to Mr. George Gray.

Enders ('05) took four species of crustaceans (*Polyonyx macrocheles* (Gibbes), *Pinnixa chætopterana* Stimpson, *Pinnotheres maculatus* Say, *Menippe* sp.?) from tubes at Beaufort. All of these crustaceans except *Menippe* were taken at Woods Hole. Usually a male and a female of the same species were found together in each tube, but several solitary individuals were captured, and once two *Pinnixæ* of each sex were found in a single tube. The results of the collections at the two localities are compared in Table I. The table shows that *Polyonyx* is the most abundant commensal at Beaufort, whereas *Pinnixa* is the most frequent at Woods Hole. Mr. George Gray, who has collected *Chætopterus* for several years at the latter place, affirms that he had never observed *Polyonyx* until about 1909, and that

SHOWING THE NUMBER OF ANIMALS FOUND IN *Chætopterus* TUBES.

Locality.	*Polyonyx macrocheles.*		*Pinnixa chætopterana.*		*Pinnotheres maculatus.*		*Menippe* sp.?	*Nereis* sp.?	*Pinnixæ* bearing *Hippuraria elongata.*		Number of *Chætopterus* Tubes, with or without Commensals.		
	♂	♀	♂	♀	♂	♀			♂	♀	Present.	Lacking.	Total.
Enders at Beaufort, N. C.	71	73	15	15	2	2	1	2	–	–	89	10	99
At Woods Hole	14	19	57	61	2	0	0	–	4	7	80	9	89

it has been increasing in numbers since then. The size of the crustaceans collected at Woods Hole was about the same as those measured by Enders ('05) at Beaufort. The maximum width of the carapace recorded for *Polyonyx* was: female, 12.5 mm.; male, 9 mm.; *Pinnixa:* female, 12.5 mm.; male, 13 mm. The proportion of tubes containing commensals was about the same at the two places.

Pinnotheres was not studied on account of its infrequent occurrence, but the behavior of *Pinnixa* and *Polyonyx* was observed in some detail. Both the latter crustaceans are thigmotropic. When placed in a dish they usually stayed close in the angles at the edge, or crawled under any objects that were present. *Pinnixæ* often clung to each other or piled up in groups. If supplied with glass tubes of suitable size, they crawled into them and there remained indefinitely.

In order to test the behavior of the commensals toward *Chætopterus* tubes an artificial tube was made in which their movements could be observed. A glass tube was bent in the form of a U and the tip of a *Chætopterus* tube slipped over each end where it was tied securely. This composi te tubewas placed upright in a rectangular glass jar filled with sand so that the glass tube could be observed through one side of the jar, though only the leathery tube tips projected into the sea water above the sand. The crustaceans were placed on the surface of the sand and their behavior observed. *Pinnixæ* usually walked to one side of the jar where they burrowed into the sand and remained for several minutes; the *Polyonyces* moved quickly to the side

of the jar and crouched on the sand. None of the crustaceans moved at once to the projecting tube tips, and sometimes they even came in contact with a tube without reacting. After a time, however, they would begin slowly exploring the surface of the sand, and, if they then came in contact with a tube, usually entered at once, whether a *Chætopterus* was inside or not. Apparently they found the tubes by accident.

In regard to the ability of the commensals to leave the tube Van Beneden ('76, p. 20) says, "On the coast of Brazil, my son found two couples of crabs in the tube of a very long annelid, narrow at the ends, and wide in the middle. The tube was too small at the end to allow them to escape. These crustaceans had, no doubt, penetrated thither before they had attained their full size. Enders ('05, p. 39) also believes that, "Once in, the crabs remain there and are later prevented through their own growth from escaping. . . . When a worm in a tube dies the crabs in the same tube die as a result of the failure of food and properly aerated water." Some tubes may be too small to allow the commensals to pass in and out, but there can be no doubt that they enter and emerge again in some cases, as the two following experiments show.

Experiment 1.—On July 19 three *Pinnixæ*, two males and a female, were placed on the sand in the jar containing the tube previously described, which contained a living *Chætopterus*. Next morning all had entered the tube; the *Chætopterus* was dead. At 2.00 p. m. two of the crabs had come out on the surface of the sand, but one still remained in the tube.

Experiment 2.—After the last experiment the tube was removed, thoroughly cleaned, and replaced in the jar with fresh sand and sea water, but no *Chætopterus* was placed in it. On July 20, at 5.00 p. m., the two largest *Pinnixæ* obtainable (male, 13 mm. wide; female, 12.5 mm.) were placed on the sand; at 9.00 a. m. the next morning the male was in the tube, and at 12.30 p. m. the female had entered. On July 22, at 3.00 p. m., a male (9 mm.) and a female (12.5 mm.) *Polyonyx* were also placed in the jar. The male entered at 3.21 and the female at 3.40 p. m. All four crabs remained within the tube until July 24 at 4.45 p. m., when I observed that the water had become foul;

the female *Polyonyx* had left the tube and was on the surface of the sand. The other three crustaceans stayed within until July 27, at about 8.00 p. m., when the male *Polymyx* emerged. The water in the jar at that time was murky, but did not have a very bad odor. On the morning of July 29 the water had some odor; the *Polyonyces* were dead on top of the sand and the *Pinnixæ* had left the tube but were alive and active.

The crabs in experiment 2 were the largest obtainable and the apertures at the ends of the tube tips were of medium size. They seemed to have little difficulty in passing in or out, though one would not think so at first glance. *Pinnixa* walked in sideways; *Polyonyx* extended its chelæ and one of them preceded the body, the other followed.

Locomotion outside the tubes was first studied in a large flat dish containing sea water. *Pinnixa* did not use its last leg when walking forward, but when going sideways used all the walking

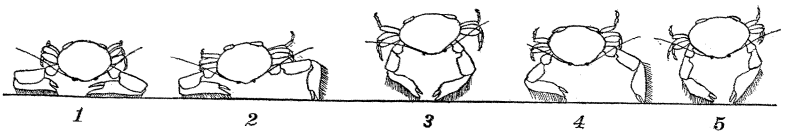

FIG. 1. Diagrams to represent the method of locomotion used by *Polyonyx* when resting on its setal fringe with its body against some object.

legs, except the chelipeds, which were hugged close against the body; it was never seen to move backward. *Polyonyx* usually moved backward when in the open and sideways along the sides of the dish. In the latter situation it always faced toward the center of the dish, or, if in haste, stood with its ventral surface against the side of the dish and walked along on the tips of its chelipeds and the bristles along their outer edges (Fig. 1). If very much hurried an animal sometimes turned on its back and flapped its abdomen, thus swimming slowly. When placed in a vertical glass tube filled with sea water *Polyonyx* kept from falling by bracing the fringe of bristles on the chelipeds and the second and third walking legs forward; the fourth leg serving as a prop behind (Fig. 7). The small fifth leg was not used. Locomotion was always sideways. In a similar situation *Pinnixa* braced with all its walking legs; the first and second were extended forward, the third below, and the fourth and fifth

backward. The largest and strongest leg, the fourth, served as a sort of hook to grasp any inequality in the wall of the tube, and the smaller fifth leg was often used in much the same way. In a horizontal tube *Pinnixa* moved sideways or stood in a position like that when on a flat surface; *Polyonyx* usually rested on the fringe of bristles along the chelipeds with its head down. *Pinnixa's* most effective locomotor organs are the fourth walking legs; *Polyonyx* uses the chelipeds most.

Pinnixa is an expert burrower, but *Polyonyx* has little ability in that line. When placed in a bowl containing sand and sea water a *Pinnixa* would scratch for a moment with all the walking

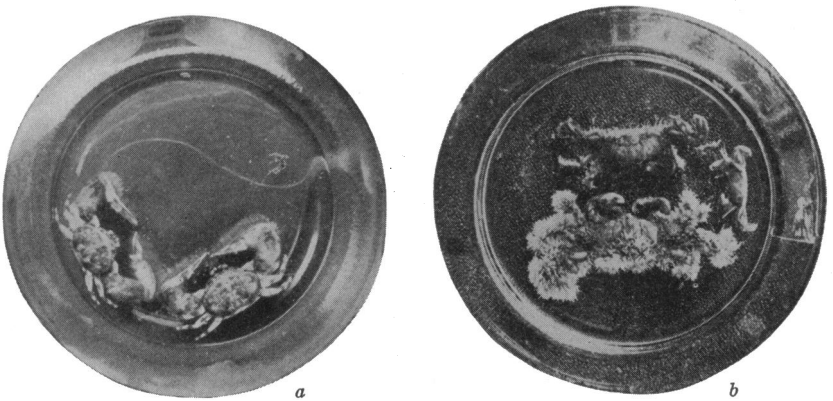

FIG. 2. *Polyonyx* and *Pinnixa* in Syracuse watch glasses. × 4/7. *a*, *Polyonyx*—male at left, female at right. *b*, *Pinnixa;* the lower individual is covered by the bryozoan *Hippuraria elongata* Osborn.

legs except the chelipeds, then stop moving the legs on one side and quickly burrow sideways by scraping the sand away with those of the other. Usually one would bury itself completely in a minute or two. If *Polyonyx* was placed in the same bowl it did not burrow, in fact was never seen to burrow, though occasionally an individual would wiggle itself down into the sand a little.

Respiration is a matter of importance to an animal that lives in a worm tube imbedded in a muddy flat. Yet *Pinnixa* apparently takes no special precautions to secure well-aerated water and is able to endure a much greater degree of foulness than *Polyonyx*. Its respiratory currents are feeble and incon-

stant both as to force and direction. In *Polyonyx*, however, such currents are strong and well adapted to life in tubes. When an individual is placed in a dish of water, a current will soon be seen to issue from beneath the anterior end. Sometimes it passes straight forward, but more often moves to the right or left,—as it would have to do if the crustacean were in a tube.

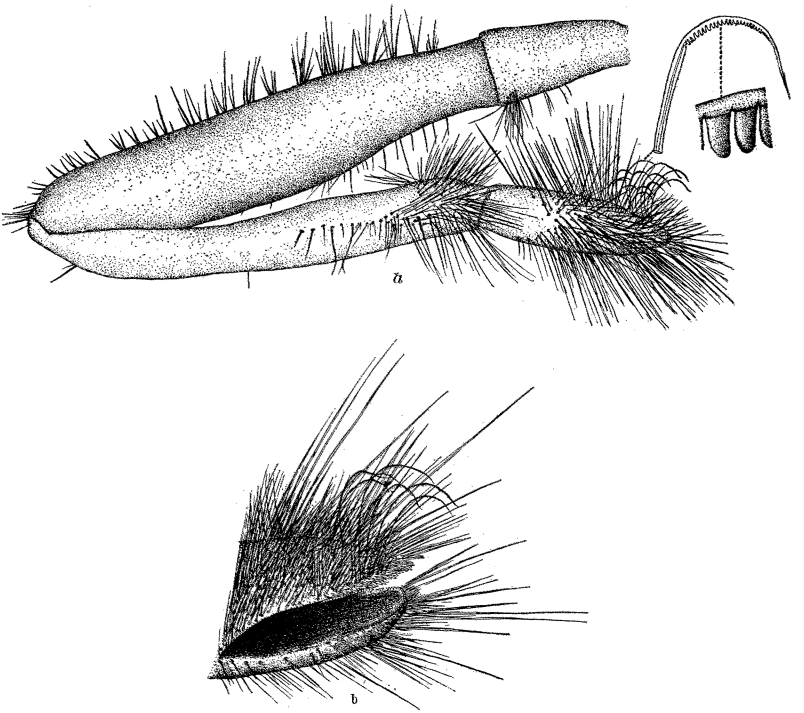

FIG. 3. Cleaning leg of *Polyonyx*. *a*, entire leg with details of pectinate setæ; *b*, chelate tip of leg.

The direction of the respiratory current in a particular individual may change frequently in a dish, but in a tube it is usually constant for hours at a time. Furthermore, several individuals in a tube together will adopt the same direction so that the water passes in one end of the tube and out the other. *Polyonyx's* antennules assume a peculiar position in relation to the respiratory current. Both are bent against the current and take such a position that the smooth ramus (Fig. 5*a*) meets it first; and if the current is changed, the position of the antennules is always

altered at once. These appendages are waved quickly at regular intervals while extended.

Polyonyx is very cleanly. The last leg is not used for locomotion, but is peculiarly modified, as in many anomurnas, to form a cleaning organ (Figs. 3, 7). The tip is chelate and is provided with peculiar pectinate and plumose setæ. The crustaceans use these appendages with great expertness; they can reach all parts of the body with them, even the interior of the gill chambers, and can frequently be seen industriously currying themselves. As a result, the body is always as smooth and clean as new porcelain. *Pinnixa* apparently takes little care for its cleanliness. Except for the mouth parts, antennæ and eye stalks, the body is usually dirty and over-grown with various organisms. A bryozoan completely covered the exposed parts of several of the individuals captured (Fig. 2*b*), a *Vorticella*-like protozoan was attached to others, and one crab was observed that carried a small clam, *Mytilus edulis* (Linnæus), attached to its last leg by byssal threads. Concerning the bryozoan Osborn ('12) says: "*Hippuraria elongata* is also a commensal living in the branchial chambers of the blue and spider crabs and on the carapace of *Pinnixa* living in the tubes of *Chætopterus*." This species is apparently not found except in association with crabs.

In most of the particulars described the two crustacean tenants in *Chætopterus* tubes showed striking dissimilarity, but their feeding habits were very much alike. Both *Polyonyx* and *Pinnixa* obtain their food by "net-fishing" (Calman, '11, p. 115) like barnacles. The "nets" in both are formed by the endopods of the third maxilliped which are well supplied with plumose setæ. A *Polyonyx* by spreading his nets (Fig. 4) can strain most of the water passing through the tube where he lives. They are extended laterally and swept together below the body. Captured food is carried against the ventral side of the body where it is scraped from the setæ of the net by the mouth-parts. *Pinnixa* feeds in a similar manner but the nets are raised above the head and swept forward and downward against the mouth. Various small organisms are captured. Eight fresh *Pinnixa* stomachs were examined on August 5 and found to contain (in order of abundance): pieces of algal filaments, diatoms, a flagellate

(*Exuvella*), fine silt, and other unidentifiable particles. Five *Polyonyx* stomachs examined August 9 contained: diatoms, silt, algal filaments, and spores or cysts. The commensals apparently feed on such organic matter as can be strained from the water passing through the worm tubes in which they live.

Enders ('05) points out that a prolonged breeding period characterizes *Polyonyx* and *Pinnixa*, and he believes this condition is due to the protection afforded by the worm tubes.

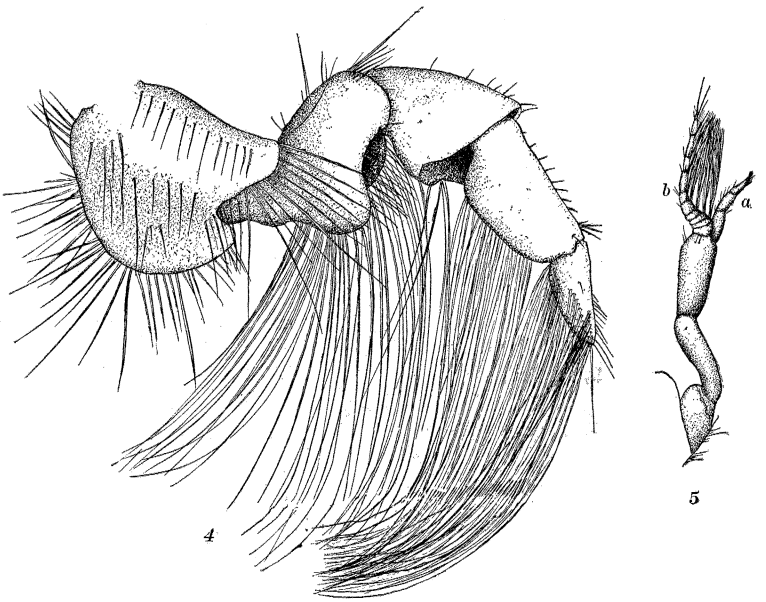

FIG. 4. The endopod of the third maxilliped of *Polyonyx*—"the fishing net." The long setæ on the four distal segments are plumose (not shown in the figure).

FIG. 5. First antenna (antennule) of *Polyonyx*.

Every female he took at Beaufort, from June 21 to October 25, bore eggs or had recently shed them. Every female taken by the writer at Woods Hole (July 18 to August 9) bore eggs or young. Four females shed their zoëa in the dishes where they were kept in the laboratory. The bluish eggs of *Pinnixa* are well protected by the broad abdomen which folds tight against the body and completely covers them. Those of *Polyonyx* are bright red; they project so that they are not concealed by the abdomen and appear as a bright mass between the body and the chelipeds when the crustacean is viewed from above (Fig. 2*a*).

The light reactions of the commensals were tested. Animals were placed in a flat dish containing sea water. This dish was barely enclosed by a box two feet long and sixteen inches wide. The box was painted black on the inside and light was admitted through an aperture two inches high across the lower side of one end. When a *Pinnixa* or a *Polyonyx* was placed in the box before a window it usually went toward the light and tried to get through the glass for a time. It soon began to wander about the dish, however, and after twenty-four hours spent most of the time in the darkest end of the box. When ten individuals of the same species were put in the dish simultaneously their behavior was essentially the same. Twenty *Pinnixæ* and seven *Polyonyx* were left together in the box several days. When the lamp was lighted before the opening of the box at night most of the crustaceans went toward it and tried to get through the end of the glass dish, but after an hour they became scattered about the dish without particular reference to the light. Mast

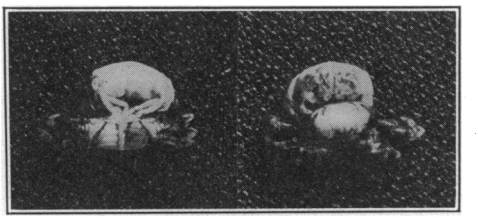

FIG. 6. *Pinnixa* undergoing ecdysis. The left-hand figure shows a ventral, the right-hand a dorsal view.

('11, p. 284) mentions several animals which, though usually negatively phototropic, may become positive for a time after mechanical or other stimulation. Apparently steady light is not, as a rule, an important factor in the daily life of *Pinnixa* and *Polyonyx*, but if confined under unnatural conditions they may go toward a light. Such reactions might enable them to escape from confinement. Both *Pinnixa* and *Polyonyx* responded readily to a decrease in light intensity. The former was very active when placed in a glass dish and kept its legs continually in motion; but if an object was passed between it and the window it became motionless at once. Though *Polyonyx* was more

sluggish it showed similar sensitiveness to shadows. Such reactions would of course help to protect these animals from predaceous enemies.

On July 24 one of the *Pinnixæ* in the "dark box" liberated a number of zoëa larvæ which swam persistently against the glass toward the light for an entire day; they were then removed.

Pinnixæ underwent ecdysis in the dishes in which they were kept; one shed on July 24 and two on August 5 (Fig. 6). They were apparently much hardier than *Polyonyx* and did not throw off their legs readily nor die if the water became foul. *Polyonyx*, like all its near relatives (Calman, '11, p. 114), readily practices autotomy, and quickly succumbs to unfavorable conditions. Its extreme cleanliness has already been mentioned.

General Discussion.

Perhaps the chief point of interest in these dissimilar crustaceans which have come to be associated with *Chætopterus* so closely that they are rarely found elsewhere lies in the similarities in physiology and structure which have enabled them to take up such a peculiar mode of life. The similarities ought to point to essential or fundamental characteristics from an ecological point of view, and the unlike features should be of less importance.

Let us first examine the differences between *Polyonyx* and *Pinnixa*. As to relationship, both are decapods, but the former belongs to the family Porcellanidæ (tribe Galatheidea, section Anomura) and is therefore not a crab despite its general appearance; the latter is a true crab of the family Pinnotheridæ (tribe Brachygnatha, section Brachyura). The Porcellanidæ use only three pairs of legs for walking, the first forming the chelæ and the last being very small and carried folded up at the sides of the body or even within the gill chambers. They are mostly found under stones along the sea shore and among corals. The family Pinnotheridæ contains many crabs which live as commensals in molluscs, worms, sea-urchins, and other animals. Their shells are often softened or membranaceous, and their eyes are very small; both these characteristics have been supposed to have arisen as a result of commensal life (Stebbing, '93, p. 100); the fifth legs are much shorter than the fourth but are used for

walking. *Pinnixa* never walks backwards, while *Polyonyx* never walks forwards; but both move sideways.

Pinnixa is very hardy and can stand foul water, as well as the indiscriminate growth of organisms on its carapace, and does not have a strong respiratory current. *Polyonyx* is not hardy, but takes every precaution to protect itself. It has a special cleaning appendage; when at rest it stands high on its setal fringe above the dirt that may collect under it; it never burrows; it has a very strong respiratory current which is deflected laterally so as to clear its abode. Apparently *Pinnixa* can endure great hardship through its great resistance, and *Polyonyx* has a number of adaptations to protect itself from contamination. The former could live almost anywhere, the latter is adapted to life in *Chætopterus* tubes or other protected situations.

The similarities between these commensals are as follows: Both are, like most crustaceans, strongly thigmotropic, and creep into crevices or tubes; they become quiet when a shadow passes over them; they feed by "net casting" after the manner of barnacles; both have a very long breeding season, producing one brood after another; and both have the last leg shortened. Their thigmotropism would easily account for their entering *Chætopterus* tubes and their feeding habits are admirably suited for the capture of food in such a situation. The quick cessation of motion when stimulated by a decrease in light might protect them from enemies when out of their tube. Enders ('05) believes that the long breeding period is an adaptation that has arisen as a result of the protected life in the worm tubes.

Shelford ('11, p. 603) says: "An animal should be associated: first, with breeding conditions; second, with the feeding conditions; third, with the conditions affecting shelter." In the present case, in fact in the case of most crustaceans, external conditions are of consequence in breeding only in limiting parents to a general region where the larva may carry on its later development, for the eggs are carried by the parent for a longer or shorter time. Some crustaceans (*Birgus*) have probably adapted their reproduction to suit a particular environment. The feeding habits of *Polyonyces* are such that they might exist anywhere in shallow water. It is apparently for protection that they have

taken up life in *Chætopterus* tubes. While this in no way disproves Shelford's statement as a general proposition, the three factors would, in the present case, come in the following order; the most important first: (1) protection, (2) food, (3) breeding. Of course, if suitable conditions for breeding were absent the crustaceans would become extinct; but given the racial habit of carrying eggs and the abundance of pelagic microörganisms in littoral waters for food, reproduction takes care of itself, is fostered, in fact, and its products are unusually abundant.

Calman ('11, p. 217), in speaking of the association of Pinnotheres with molluscs, says, "The case is, indeed, an example of the difficulty of defining these two terms (commensal, parasite). At all events the Pinnotherid crabs show one of the characteristics of parasites in being to some extent degenerate in their structure. The carapace and the rest of the exoskeleton, no longer needed for protection, have become soft and membranous, and the eyes and antennules, the chief organs of sense, are very minute. As in many parasites, also, the eggs are very numerous, and the abdomen is very broad and deeply hollowed out for their reception." To this list I may also add that *Pinnixa's* fourth and fifth legs are used as hook-like claws for holding on, like the organs of fixation in many parasites.

There is no question but that the two commensal crustaceans discussed gain from their association with *Chætopterus*, but it is doubtful if the worm is benefited.

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Explanation of Plate I.

Fig. 7. Section of a *Chætopterus* tube in the sand. It contains a worm in the lower part. On the left a male (above) and a female *Polyonyx* are clinging to the wall of the tube. The male is cleaning his back with the comb on the tip of his last leg; the female rests with her ventral side toward the observer. Drawn from life by Miss Barbara Bradley.